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White Paper

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TITLE: GRIZZLY BEARS AND WHITEBARK PINE IN THE GREATER YELLOWSTONE ECOSYSTEM. FUTURE STATUS OF WHITEBARK PINE: BLISTER RUST RESISTANCE, MOUNTAIN PINE BEETLE AND CLIMATE CHANGE

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Introduction

The U.S. Court of Appeals for the 9th Circuit in November 2011 upheld the lower court decision vacating the delisting rule for grizzly bears. An important reason for the 9th Circuit Court decision was due to potential impacts of the decline of whitebark pine as a food source for grizzly bears in the Greater Yellowstone Ecosystem (GYE). An interdisciplinary, interagency team of federal and state agency members was assembled to summarize available information regarding the potential impacts of changes in whitebark pine, other food resources, anthropogenic factors, and density dependence on GYE grizzly bears. Information from this team will be provided to the U.S. Fish and Wildlife Service to inform their decision as to whether delisting this population is appropriate. The intent of this white paper is to provide a chapter for a compilation of manuscripts being drafted as part of this comprehensive research effort. The general theme of this paper is whitebark pine ecology with a special emphasis on the species' future status relative to blister rust resistance, mountain pine beetle trend predictions, and climate change. The target audience includes federal and state partners of the Interagency Grizzly Bear Executive Committee and its Yellowstone Ecosystem Subcommittee.

The primary approach taken in developing this paper is a literature review building on the research and monitoring efforts since the publication of the whitebark pine range-wide restoration strategy (Keane et al. 2012). In addition, data available from the Inland West Whitebark Pine Genetic Restoration Program (Mahalovich and Dickerson 2004) and the USDA Forest Service, Forest Health Protection Aerial Detection Survey Program (USDA 2012a, 2012b, 2012c) follow each topic to provide current information specific to the GYE, but which may not be available in the published literature. Sampling methodologies and empirical data are anticipated to provide a different perspective than the hypotheses of current status and future trends in the published literature, but also complement information provided by the Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG) (2012, 2013).

The context of each topic: blister rust resistance, mountain pine beetle trends, and their correlated response, will vary along a spatial hierarchy from the landscape to local scales to family and individual-tree dynamics. Overlaying this spatial hierarchy is a discussion of the temporal variability associated with the climatic factors driving these biological stressors.

Whitebark pine is both a keystone (Mills et al. 1993, Paine 1995, Callaway 1998) and foundation (Ellison et al. 2005) species. As a keystone species, whitebark pine maintains subalpine biodiversity and its nuts provide a nutritional source of food for several wildlife species (Lorenz et al. 2008). As a foundation species, whitebark pine protects watersheds and promotes post-fire regeneration. It occurs from 37° to 55° N latitude, 107° to 128° W longitude, from subalpine to treeline, and elevations from 900 to 3660 m. Within the GYE it is occurs on 1 million ha (10% total acreage) from 42° to 46° N latitude, 107° to 112° W longitude, with a more narrow elevation range of 2,500 to 3,060 m. Whitebark pine is one of six conifer species in the GYE occurring in pure stands on exposed sites at high elevations and in mixed-conifer stands just below timberline (Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee (GYCCWBPS) 2011).

Severe population declines in whitebark pine communities are attributed to blister rust (*Cronartium ribicola* J.C. Fisch. in Rabh.), mountain pine beetle (*Dendroctonus ponderosae*), fire suppression, forest succession, wildland fire, and climate change. The relative importance of each threat acting alone or in concert varies by region, population structure, including age of cohorts. Large-scale mortality within the GYE is driven by a recent mountain pine beetle outbreak, wildland fire, and to a lesser extent, blister rust. Mortality among the 235 whitebark pine plus trees (cone-bearing individuals in the field exhibiting phenotypic resistance to blister rust and possessing 30 percent or more live-green crown) designated in the genetics program is 25%, with 90% due to mountain pine beetle (Mahalovich 2012). Whitebark pine is currently listed as a species under consideration for protection under the Endangered Species Act (1973) (US Fish and Wildlife Service 2011). Range-wide, the species is assessed as endangered on the IUCN Red List (Mahalovich and Stritch 2013).

This white paper is divided into four sections followed by a statement of the projected outlook for whitebark pine in the GYE. A brief clarification of terminology and background of blister rust infection in five-needle pines introduces the first topic of blister rust resistance in whitebark pine.

Blister Rust Resistance

Definitions

Susceptibility and infection or resistance and immunity are key terms that are frequently used interchangeably. This has led to confusing and conflicting expectations and performance of current and future conditions of whitebark pine.

Susceptibility is defined as an individual lacking the ability to resist a pathogen (see page 14 for a more explicit definition within the context of an artificial inoculation trial). **Infection** is defined when the germinating blister rust basidiospore has penetrated a stomate (Figure 1), followed by colonization of tissue by mycelium. In a susceptible host this is followed by canker development in branch and stem tissue. Observed responses to infection include needle spotting (cell chlorosis is the first sign of changes in needle tissue), branch swelling and bole swelling with orange margins (due to pine cell color changes plus the color of the rust fungus), followed by the development of diamond-shaped cankers. Presence of blister rust does not imply eminent mortality; six of seven rust resistance traits require an individual to become infected before genes involved in rust resistance are expressed. Because of this, sufficient time must elapse before an individual infected with blister rust can be determined to be susceptible or resistant.

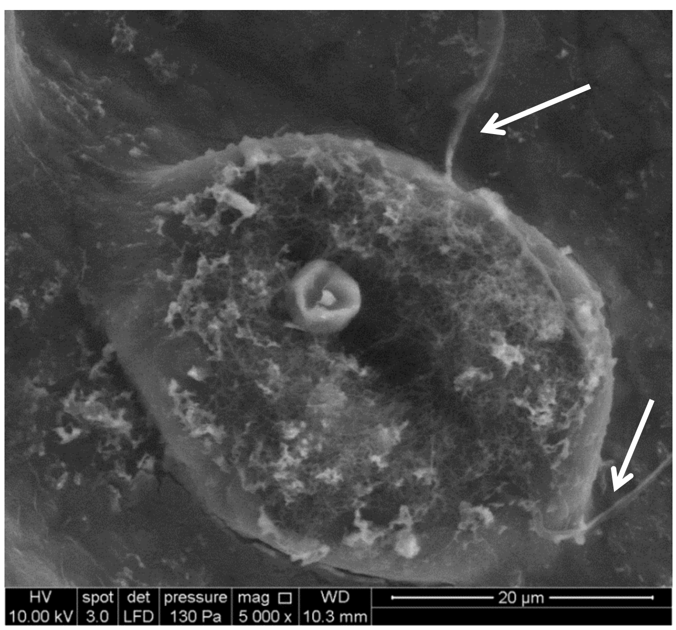

Figure 1. Field emission scanning electron microscopy image of spent basidiospore lodged in central cavity of a whitebark pine stomate from plus tree 6517 Pilot Knob, Idaho; two basidiospore germination tubes are in visible on the right (white arrows) (rev 9-23-2011). Photo credit M.F. Mahalovich.

Resistance is defined as a tree's ability to tolerate or counteract the presence of infection. Mechanisms of resistance are presumed to involve a genetic component. A resistant individual displays symptoms of infection, however, the tree is able to survive and reach reproductive maturity. Resistance to blister rust in five-needle white pines is categorized as polygenic and Mendelian resistance, ontogenetic resistance, and major gene resistance (MGR) (i.e., gene-for-gene action). Some trees of sugar pine (*P. lambertiana* Douglas., *Cr1*), coastal populations of western white pine (*P. monticola* Dougl. ex D. Don, *Cr2*), southwestern white pine (*P. strobiformis* Engelm., *Cr3*), and limber pine (*P. flexilis* James*, Cr4*) exhibit MGR (Kinloch and Dupper 2002, Schoettle *in press*). Trees possessing MGR exhibit a hypersensitive reaction (HR) in needle tissue (i.e., the margin of the needle spot is surrounded by necrotic tissue) when artificially inoculated with blister rust. Trees with HR do not develop cankers. Mendelian segregation ratios in HR trees indicate a single, dominant allele for resistance that is specific to each host species, and is limited to its effectiveness against only one genetic variant in the rust. Whitebark pine, foxtail pine (*P. balfouriana* Balf.*),* Great basin bristlecone pine (*P. longaeva* D.K. Bailey*)*, Rocky Mountain bristlecone pine (*P. aristata* Engelm.), and interior populations of western white pine do not possess MGR (Kinloch and Dupper 2002, M. Mahalovich, U.S. Forest Service, unpublished data). MGR by some authors is also considered a form of immunity.

Immunity implies an individual is capable of resisting infection at a very early stage, preventing or eliminating infection by a preformed or early-induced physiological mechanism, that may cause death of some host cells and limits pathogen spread. An immune tree remains symptom-free throughout its life (i.e., no needle spotting, no branch flagging, no cankers, and no broken tops attributed to girdled stems). In some immune western white pine trees, epicuticular wax or biochemical differences in wax composition suppress mycelium germination and growth in the stomatal chamber, and these trees do not develop cankers (Woo 2002, Smith et al. 2006).

Blister rust infection

Blister rust has caused significant mortality of five-needled pines in North America and widespread disruption of ecosystems where these pines were once keystone species (Maloy 1997). Blister rust was introduced into the west coast of North America in the early 1900s on infected eastern white pine (*Pinus strobus* L.) seedlings grown in France (Hunt 2009). One documented introduction site was Point Gray near Vancouver, B.C. (Mielke 1943); however, to account for the long distance spread and build-up of inoculum by 1913, it has been suggested there were other introduction sites along the west coast of North America (Hunt 2009). Although blister rust has been in North America for a relatively short time, the pathogen shows a great plasticity in host-species utilization (Richardson et al. 2007).

The life cycle of blister rust has five spore stages, two specific to five-needle pines and three on its alternate hosts. Alternate hosts include most shrub species of the genus *Ribes* spp. (family *Grossulariaceae*), *Pedicularis* racemosa Dougl. Ex Benth., *Pedicularis bracteosa* Benth., and *Castilleja miniata* Dougl. Ex Hook. (family *Orobanchaceae*) (Patton and Spear 1989, McDonald and Hoff 2001, McDonald et al. 2006, Zambino et al. 2007, Geils et al. 2010) (Figure 2). New alternate hosts continue to be identified in certain species within the genera *Mentzelia* and *Loasa* (family *Loasaceae*) (Kaitera and Hiltunen 2012). *Mentzelia lindleyi* Torr. & A. Gray is native to Arizona and California and cultivated as an ornamental. *Loasa triphylla* Juss. is native to South America and cultivated as an ornamental. The blister rust life cycle becomes more complex as the list of new alternate hosts increases. Basidiospores predominantly from *Ribes* spp. are transmitted to pines in late summer or early fall (August to October). Early frosts and drier conditions in the GYE limit the transmission period from August to September. Blister rust is considered a cool weather disease, where basidiospore germination and pine needle infection occurs between 0° to 20°C, requiring 48 h with conditions near 100% relative humidity (Van Arsdel et al. 1956, Van Arsdel 1967). The delicate basidiospores germinate to penetrate

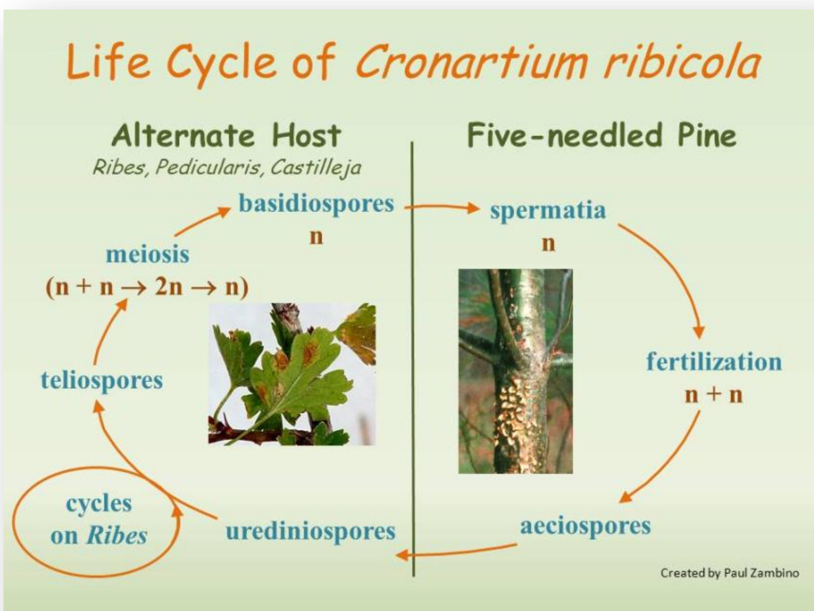

Figure 2. Life cycle of blister rust in five-needle pines and its alternate hosts *Ribes, Pedicularis and Castilleja* spp. (source P. Zambino, U.S. Forest Service, Forest Health Protection).

pine needle stomata. If a tree does not possess genetic resistance to blister rust, sporulating cankers girdle branches, flagging (dead needles) occurs, progressing to branch dieback. In the case of bole cankers, girdling results in top dieback followed by tree death.

On susceptible trees, rust hyphae then colonize needle parenchyma and vascular tissue spreading infection into the phloem, cambium, and xylem of branches and stem boles (McDonald and Hoff 2001, Hudgins et al. 2005). Cankers become apparent as early as two years following infection. Cankers later produce pycnia (spermagonia) from just under the bark epidermis. These produce pycniospores that are spread by insects, causing fertile hyphae in other pycnia to be fertilized and the rust to cross.

The following year, aeciospores erupt from deep in the phloem near the fertilized pycnia. This disrupts the phloem and causes part of the phloem to die. The small, light aeciospores infect three alternate hosts through their stomata; in addition to aeciospores, urediniospores can infect associated species of *Pedicularis* or *Castilleja*. Aeciospore transmission to *Ribes* spp. has been estimated to be as far as 300 km (Fujioka 1992) to 500 km during wave years (Mielke 1943). Wave-year events can either be a significant local intensification of rust infection or a long-distance jump of blister rust. Wave years need not be particularly wet, however 'dry' events are typically preceded by one or two wet years (Fujioka 1992).

Ureodinospores may be produced on and reinfect the alternate hosts and increase infected leaf surfaces. Columns of hair-like teliospores form on the underside of infected leaves of alternate hosts in fall or other periods of cool, wet weather. Teliospores germinate to produce basidiospores, which are forcibly ejected into cool, wet air to infect the host pine species. The relative contribution of *Pedicularis* or *Castilleja* to basidiospore production is still relatively untested in North America, but is inferred at some high-elevation western white pine (*Pinus monticola* Dougl. ex D. Don) sites from dense cover and infection in these hosts, and from infections in a small sample of western white pine seedlings of unknown origin (McDonald et al. 2006). Basidiospore production in herbaceous plants is still relatively untested and no contrasts of effectiveness or rates of infection have been performed in a controlled environment among the alternate hosts relative to pine. As such, there is no definitive proof that basidiospores produced on *Pedicularis* and *Castilleja* directly infect whitebark pine, but is inferred from infections achieved in a small sample of western white pine seedlings of unknown origin (McDonald et al. 2006).

Regional geography and local physiographic features dictate whether pine infections originate predominately from sources within the pine stand (local spread) or from distant sources (long-distance dispersal) (Zambino 2010).There are two modes of blister rust dispersal: 1) Basidiospores may be dispersed by diffusion at the local scale, where the density of spores for

Box 1. Gradient Modeling

Helmbrecht et al. (2007) developed a 1-km² resolution spatial layer of blister rust infection levels for whitebark pine using gradient modeling. Plot-level surveys of whitebark pine and percent infection documented in the USDA Forest Service Whitebark-Limber Pine Information System database http://www.fs.usda.gov/detailfull/r1/forest-grasslandhealth/?cid=stelprdb5157913&width=full *were selected to build a point feature class of field plots. The objective was to identify key environmental gradients available as spatial data known to govern rust propagation. Climatological summaries of meteorological observations were obtained for each location using DAYMET. Using the sample function in ArcGIS, a table of 869 usable plots was built of gradient values (predictor variables) and rust infection levels (response variable). A predictive landscape model was developed using the random forest method using R statistical package, followed by mapping model results to the range of whitebark pine. The model explained 58% of the variation in rust infection data. Approximately 25% (1.4 million ha) of whitebark pine potential habitat was modeled to have potential infection greater than 50%. Spatial mapping (Figures 3 and 4) would benefit from reanalysis of more current rust infection levels and a larger sample size (R. Keane, personal communication).*

deposition and infection from a single source declines in magnitude with distance according to the square-root function. In this mode, basidiospores usually travel only a short distance, averaging 300 m since the delicate spores are vulnerable to desiccation and sunlight (Kinloch 2003). Local spread (diffusion) and intensification of blister rust in five-needle pines progresses concentrically and relatively slowly (Kinloch 2003). 2) Long distance flow can occur at multiple scales as a result distinct air masses with a combination of laminar flow and disruption by turbulent mixing (Van Arsdel et al. 2006). The range of basidiospore dispersal also varies by position of blister rust cankers within an infested crown. Hunt (1983) found within western white pine stands in British Columbia, cankers near the ground resulted from *Ribes* inoculum produced in the stand, whereas cankers high in the crown resulted when inoculum from a distant source was carried into the stand by down-slope air flow (Hunt 1983). Thus, average distance estimates of basidiospore transport range from 15 m to 27 km, where patterns of pine infection and distances of effective dissemination also vary from year-to-year with annual variation in the weather (reviewed in Zambino 2010). Lastly, moist air masses in late summer form the backdrop of wave years, where basidiospores can survive traveling farther over wider geographic areas (Van Arsdel 1967).

There are no known virulent or aggressive races of blister rust on various forms of resistance in the Inland West. The low percentage of polymorphic loci is consistent with that expected for an invasive species with a single introduction (Kinloch et al. 1998a, Richardson et al. 2008). Genetic diversity and differentiation among populations of blister rust are generally low (8% - 9.6%) and genetic distances are not correlated to geographic distance; the largest genetic distance is between Happy Camp, California, and other populations sampled in western North America (Kinloch et al. 1998a, Richardson et al. 2007). While sites from northern California (Happy Camp and Klamath Mountains) were distinct (Richardson et al. 2008), other populations in western North America were distributed without pattern, characteristic of a metapopulation structure largely driven by frequent founder events and genetic drift (Kinloch et al. 1998a, 1998b). Pine hosts containing polygenic resistance have no apparent impact on changes in the genetic diversity of blister rust (Richardson et al. 2008). However blister rust populations on a continental scale, are distinct between eastern-central and western North America, with greater genetic diversity in the east. More widespread introductions in the east and physical and biological barriers to gene flow are attributed to be causes of this differentiation (Hamelin et al. 2000).

Blister rust infection levels in whitebark pine (Figure 3) range from 0 to 100% in the U.S. Northern Rockies (Kendall and Keane 2001, Kinloch 2003, Schwandt 2006). Projected blister rust levels using gradient modeling (Helmbrecht et al. 2007, Box 1) range from 0% to 97% (Figures 3 and 4). The highest rust infection levels correspond to introduction sites in whitebark pine habitat type ca 1925 (McDonald and Hoff 2001) in northwestern Montana, which are also areas of high summer and fall moisture at appropriate temperatures for infection in pines and alternate hosts (P. Zambino, personal communication) (Figure 3). Northwestern Montana is also home to the most rust-resistant whitebark pine populations (Mahalovich et al. 2006).

Spatial variation in blister rust infection levels is referred to as site hazard where microclimatic conditions, *Ribes* spp. proximity, and *Ribes* spp. density determine hazard rating. Hazard can be quantified as the proportion of infected trees, percent mortality, or the number and severity of cankers (Brown et al. 1999, Burns et al. 2008). It is not uncommon for understory and overstory hosts to have different hazard ratings at the same location. Hazard rating in the genetics program is expressed as the proportion of infected overstory (<50% low hazard, 50-75% moderate hazard, and >75% high hazard, Mahalovich and Dickerson 2004). High blister rust infection levels in the host population equates to high blister rust hazard (Hagle et al. 1989, Hoff and Hagle 1990).

Rates of blister rust infection and subsequent mortality in whitebark pine north of the Cabinet-Yaak-Selkirk recovery zone averaged 3% per year between 1996 and 2009. Although live-tree infection was not related to elevation, mortality declined with increasing elevation (Smith et al.

2013). Mortality rates from blister rust from 1971-1991 in western Montana average 2.1% per year (Keane and Arno 1993).

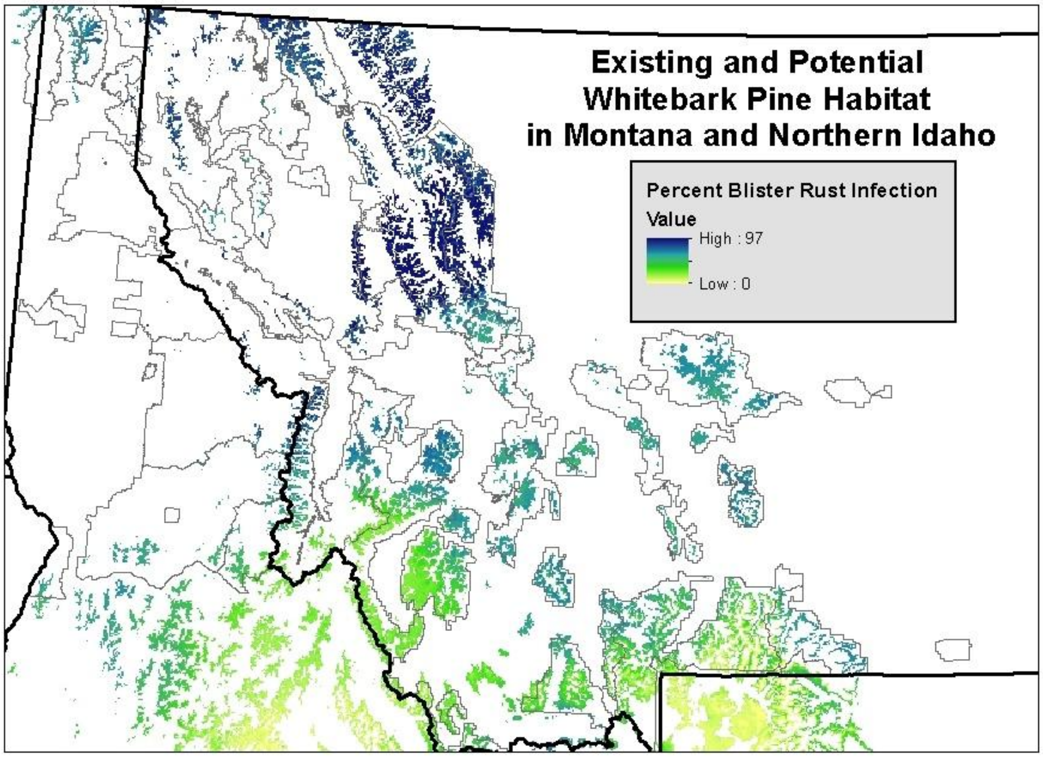

Figure 3. Modeled projections of white pine blister rust infection levels from low (0 yellow shading) to high (97 dark blue), as mapped in existing and potential whitebark pine in Montana and northern Idaho through 2007 (Helmbrecht et al. 2007).

Genetic diversity assessed with AFLP (Amplified Fragment Length Polymorphism) genetic markers in western white pine populations grown on a low hazard site had higher heterozygosity and twice as many unique alleles compared with a population grown on a high-hazard site (Kim et al. 2003). The relationship of high genetic diversity and low rust infection levels are supported in whitebark pine, whereby 63% of the genetically diverse populations within the Northern Rockies (Mahalovich and Hipkins 2011) are from low rust infection areas (Helmbrecht et al. 2007, M. Mahalovich, U.S. Forest Service, unpublished data) and 34% of those areas originate within the GYE.

Blister rust damage includes branch and top dieback from cankers girdling tree boles and branches, reproductive failure, and tree mortality. Branch and top dieback reduces photosynthetic biomass and cone production. Severely damaged trees can survive for years, but with reduced cone-bearing potential (McKinney and Tomback 2007, McKinney et al. 2009, Tomback and Achuff 2010). The reduction in cone production and increased variability in masting events due to an ineffective pollen cloud (i.e., stand density of ≤10 pollen-producing trees per acre) has serious implications in terms of providing a reliable food source for wildlife (Lorenz et al. 2008). Kinloch (2003) argues that the most insidious impact of blister rust is its destruction of host natural regeneration, which consequently alters natural succession. Hoff and Hagle (1990) and Koteen (2002) showed infected saplings generally die within three years.

Introduction into the GYE

The western introduction of blister rust is attributed to infected seedlings shipped to Vancouver, British Columbia in 1910 (Hunt 2009). Subsequent spread of blister rust differed by region, landscape and site. Blister rust reached whitebark pine ecosystems in northern Idaho and northwestern Montana by 1925 (McDonald and Hoff 2001) and was later identified in 1937 in the Bear Creek drainage on the Gallatin National Forest (NF) (Kendall and Asebrook 1998). The spread of blister rust was early and rapid in western white pine habitat types due to highly susceptible *Ribes* spp. and favorable climates. Even with adequate winds, the spread of blister rust into higher mountains east or south was delayed or slowed because of cooler temperatures needed for *Ribes* spp. infection, fewer generations of the rust cycle, and shorter growing seasons (Van Arsdel et al. 2006). Berg et al. (1975) found that blister rust in whitebark pine decreased with elevation, with 92% of all infections below 2,591 m.

Current infection levels within the GYE average 20% (GYWPMWG 2012) and range from 20-30% (GYWPMWG 2013). Symptoms of canker presence, branch flagging, broken tops, rodent chewing, roughened bark, and oozing sap are the focus of field monitoring (Hoff 1992) on trees >1.4 m tall (GYWPMWG 2012, 2013); as symptoms of needle spotting, premature needle shed of entire fascicles and fungicidal short shoot responses (Appendix 3) are difficult to assess outside of controlled, environmental conditions. Blister rust incidence and severity continues to increase across the western United States and within the GYE (Bockino 2008; Larson 2011, Bockino and Tinker 2012, GYWPMWG 2012, 2013). Smith and Hoffman (2001) found mean summer precipitation, average tree diameter, and elevation were the most important variables in logistic regression models for blister rust presence and intensity in whitebark pine in southern Idaho and western Wyoming. Using those same data to produce Figure 3 and extending the map into northwestern Wyoming (Helmbrecht et al. 2007), Figure 4 represents model projections of blister rust infection levels in susceptible stands within the GYE through 2007 (note the color scheme is different from the maximum infection level of 97% in Figure 3).

Seed-source origin data for whitebark pine plus trees are collected at the time phenotypically rust-resistant cone-bearing trees are designated in the genetic restoration program (Mahalovich and Dickerson 2004). Along with the individual-tree data, these stand or area data

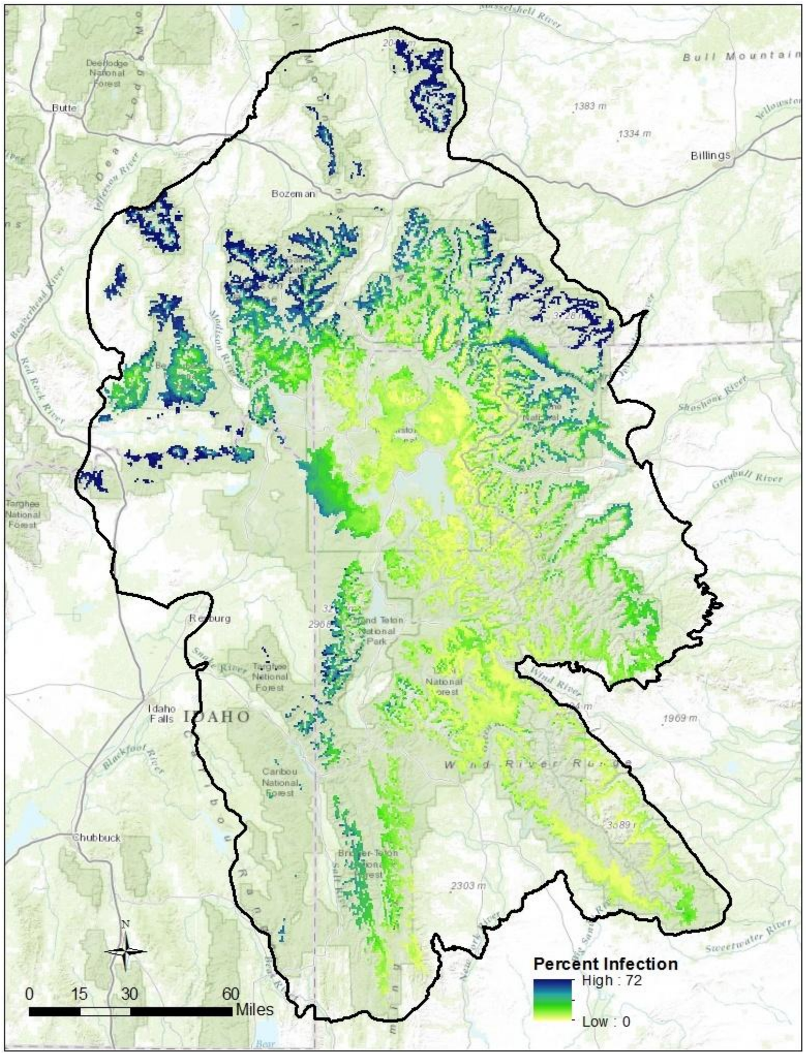

Figure 4. Modeled projections of white pine blister rust infection levels from low (0 yellow shading) to high (72 dark blue) as mapped in existing and potential whitebark pine in the GYE through 2007 (Helmbrecht et al. 2007, GIS support for GYE graphic E. Karau).

are used to characterize several adaptive traits and molecular markers, estimate genetic parameters (additive genetic variation, heritabilities, correlations among traits, Q-statistics), develop regression models to characterize patterns of variation across the Northern Rockies and individual seed zones, assign an adaptive strategy, develop seed transfer guidelines, and make elite tree selections for seed orchard establishment (Mahalovich et al. 2006, Mahalovich and Hipkins 2011, Mahalovich *in prep*). The 100-tree survey per stand (Appendix III) provides information on percent blister rust infection, average canker counts, and percent mountain pine beetle. These surveys are not part of an annual monitoring program to assess trends. However, plus tree designations per stand occur at random rather than as a stratified sampling protocol and thereby provide an average, annual incidence of percent blister rust, canker counts, and percent mountain pine beetle (Table 1). Among 76 sampled locations representing 2,610 ha within the GYE, the average blister rust infection level from 2001, 2003-2012 among the 235 plus trees was 62.6% (± 35.2%) with the highest infection levels in the northwestern and northern sections of the GYE (Figure 5). The average rust infection level among these areas was twice as high as the 176 transects of the Greater Yellowstone White Pine Monitoring Working Group (2012, 2013). There is no known overlap in sampled locations between the two data sets. A possible explanation for the difference in infection levels may be related to geography and locations sampled within each of the four panels. Blister rust infection levels by year suggest the possibility that infection levels can decrease over time (Table 1). Consistent with earlier research (Berg et al. 1975), as elevation increased blister rust infection decreased (r = -0.19, p < 0.0001) (M. Mahalovich, U.S. Forest Service, unpublished data).

Table 1. Annual blister rust infection, number of cankers per tree and mountain pine beetle incidence based on 100-tree surveys among 76 geographic areas represented in the GYE whitebark pine genetic restoration program (M. Mahalovich, U.S. Forest Service, unpublished data).

Damaging Agent	2001	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
Blister rust infection (%)	84.2	65.4	67.0	44.4	62.3	42.3	91.2	62.0	42.8	54.4	52.7
Average number of cankers per tree	8.1	13.2	4.0	8.7	4.1	3.3	23.3	6.5	3.4	6.8	12.3
Mountain pine beetle (%)	20.4	18.9	0.0	8.1	21.1	8.6	10.3	30.5	39.1	69.1	1.2

The average number of cankers per tree among the 76 locations was 9.6 (± 13.2), with the highest canker counts in the northwestern and northern sections of the GYE (Figure 6). Again, as elevation increased, average number of cankers decreased (r = 0.31, p < 0.0001) (M. Mahalovich, U.S. Forest Service, unpublished data). Annual blister rust infection and canker counts are discussed in more detail in the section "*Correlated response*" (page 23).

Blister rust infection levels by year suggest the possibility that infection levels can decrease over time (Table 1). Infection levels and mortality will likely not increase unless a virulent strain of rust is introduced, waves years, localized weather events, or micro-climatic changes once again favor the infection cycle.

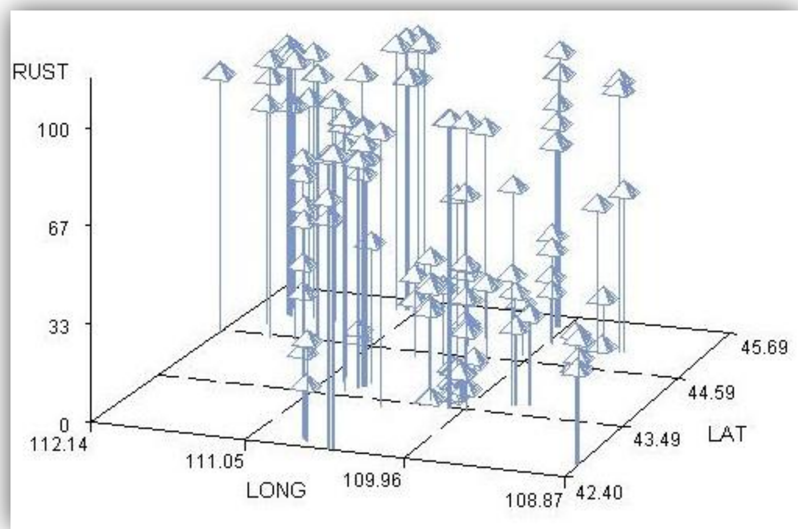

Figure 5. Percent blister rust infection levels (RUST) 62.6% (± 35.2%) among 76 geographic areas represented in the GYE whitebark pine genetic restoration program 2001, 2003-2012 (M. Mahalovich, U.S. Forest Service, unpublished data).

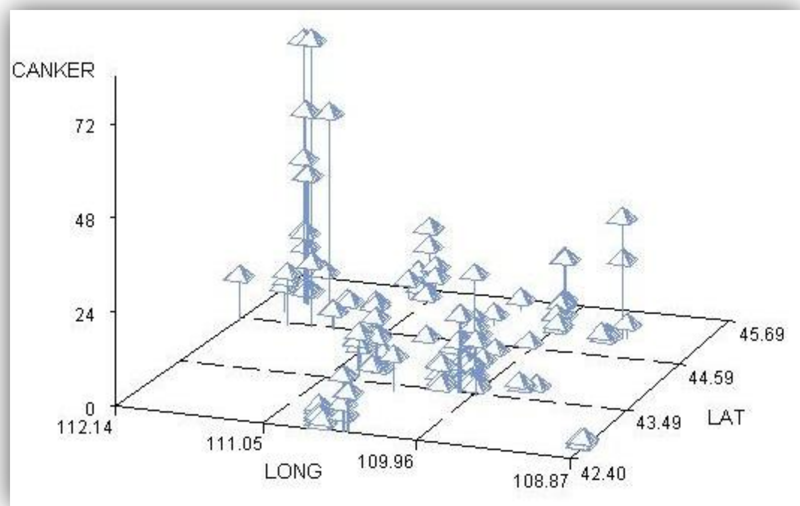

Figure 6. Average blister rust canker counts per tree (CANKER) 9.5 (± 13.2) among 76 geographic areas represented in the GYE whitebark pine genetic restoration program 2001, 2003-2012 (M. Mahalovich, U.S. Forest Service, unpublished data).

Nature of rust resistance

For six of seven rust-resistance traits (needle shed, short shoot, bark reaction, canker tolerance, spot count per linear meter, early stem symptoms, Appendix III) a tree must become infected to identify resistance. One of the seven traits, no-spotting, is an **immunity** trait that occurs in very low frequency (Mahalovich 2010). Although the frequency in the population and histograms of individuals within families suggests a single-gene recessive, it is also not major gene resistance (i.e., gene-for-gene action between whitebark pine and blister rust). Indeed, tests for major gene resistance for blister rust are negative in whitebark pine (Kinloch and Dupper 2002). In the absence of molecular markers for candidate genes, the genetic mechanism of single-gene recessives for no-spot, needle shed, and short shoot resistance traits can only be confirmed through full-sibling and selfed crosses followed by blister rust screening. The remaining traits, due to the distribution of individuals within families, behave more like polygenic inheritance. Response to selection for all traits is measured as a metric trait and analyzed by quantitative genetic statistical procedures. A minimum of 50% infection is needed to detect differences among families (seedlings of open-pollinated plus trees) and a minimum of 80% spotting is needed to assign individual-tree rust resistance traits.

Rust resistance occurs in needle, branch and stem tissue. Although the exact rust resistance mechanisms in whitebark pine are unknown, they can be inferred from western white pine (Bingham et al. 1971). Subsequent pilot rust screenings (2004-2012) of whitebark pine (M. Mahalovich, U.S. Forest Service, unpublished data) confirm these traits are repeatable and present themselves over time in a consistent fashion. The mechanisms of resistance are sequential, where resistance caused by one mechanism prevents any subsequent mechanisms from acting (Hoff et al. 1980). Due to this sequential nature of infection and expression of resistance, only one resistance type (no-spot, needle shed, short shoot, or bark reaction) can be observed per seedling. Susceptibility cannot be strictly based on spotting, as seedlings can either shed infected needles, shed short shoots, or wall off subsequent cankers from further development with callus formation. Similarly, susceptibility cannot be strictly based on canker presence as some trees can later develop callus to wall off further canker development with later canker death (bark reaction resistance trait). **Susceptibility** in an artificial inoculation trial is defined as the presence of spot symptoms on secondary needles, whereby a seedling is not scored as having the no-spot, needle shed, short shoot or bark reaction resistance traits.

All age classes of whitebark pine are susceptible to blister rust, however, conditions are more favorable for rust infection near ground-level because relative humidity is higher and needles stay wetter for longer periods of time. Primary needles are more susceptible than secondary needles and younger trees are more susceptible than grafts or older trees. Young trees have branches closer to the ground, thereby facilitating infection. Thus, tree girdling by developing cankers is more lethal in the smaller, main stem of young trees.

Ontogenetic blister rust resistance in several white pine species increases with host age (Patton 1961, Bingham 1972b, Kinloch and Byler 1981, Hunt 2005). Bingham (1966) referred to blister rust as a 'juvenile disease' due to the difficulty in artificially inoculating older material in the field or grafts of older material brought into nursery environments. Correlation analyses of blister rust infection and age of plus trees within the GYE support ontogenetic resistance: as infection decreases, plus tree age increases with r =-0.37, p<0.0001; as rust resistance increases, plus tree age increases with r= 0.27, p<0.0001 (M. Mahalovich. U.S. Forest Service, unpublished data).

Rust resistance in the Northern Rockies

Seedlings from a very limited number of families from northern Idaho established the first rust resistance measure of 33% for whitebark pine (Hoff et al. 1980). Beginning in the late 1990s, the rust screening protocol for western white pine (Mahalovich 2010) served as the template for identifying and harnessing blister rust resistance in whitebark pine (Mahalovich and Dickerson 2004). Drawing from a broader sample of 110 families from northern Idaho, Montana, eastern Washington, and northwestern Wyoming, rust resistance in the Northern Rockies is 47.4% (Figure 6) (Mahalovich et al. 2006). Heritability, expressed as a ratio of the additive genetic variation or that portion of the genetic variation that can be passed on to the next generation, divided by the total phenotypic variation, ranges from a value of 0 to 1. The family heritability for rust resistance is 0.68, indicating whitebark pine has moderate levels of rust resistance that can favorably respond to selection and breeding.

Rust resistance in the GYE

An earlier estimate of 10% blister rust resistance has been quoted for whitebark pine in the GYE. This percentage was noted in earlier drafts of the GYA Whitebark Pine Strategy (GYCCWBPS 2011). After reviewing Hoff et al. (1980) and investigating publications of Brohun Kinloch (retired, USDA Forest Service, Pacific Southwest Experiment Station) for the Kinloch (2003) citation, no inoculation trials or publications have been identified as the basis for this 10% figure. The final WBP GYA strategy still includes the Kinloch (2003) citation in the body of the text, but the reference is omitted in the literature cited section.

The first artificial inoculation trial and cold hardiness testing (1999-2005) composed of seedlings from the GYE (19 plus trees) was performed at Coeur d'Alene Nursery, Coeur d'Alene, Idaho (Mahalovich et al. 2006). From this trial, blister rust resistance in the GYE is 28% (Figure 7). The family heritability for rust resistance is 0.70 indicating whitebark pine has moderate levels of rust resistance in this region that can also favorably respond to selection and breeding.

A more recent rust screening at Coeur d'Alene Nursery (Cycle 1, 2008-2013) includes progeny from 113 of the 235 plus trees within the GYE (Figure 8). Final rust inspection data obtained September 2013, characterize rust resistance from this more representative sample at 9% (M. Mahalovich, U.S. Forest Service, unpublished data). The most rust-resistant plus tree is 6863 at Apex Trail in Grand Teton National Park and the most rust-susceptible plus tree is 6145 at Picket Pin Mountain on the Custer NF. The family heritability for rust resistance is 0.72.

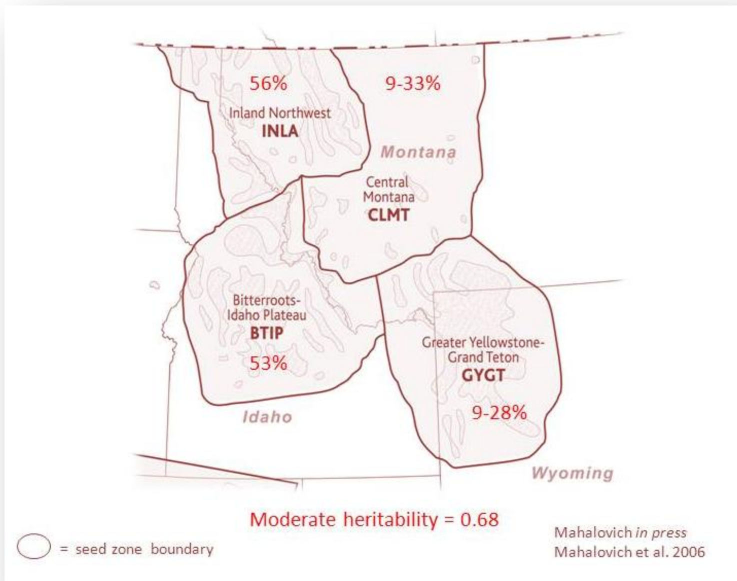

Figure 7. Whitebark pine blister rust resistance levels in the USDA Forest Service, Inland West Genetic Restoration Program (Mahalovich et al. 2006, Mahalovich *in prep*).

Current rust-resitance levels in the GYE are in the range of 9 to 28%. Rust-resistance levels established in artificial inoculation trials, like heritability values, are specific to that trial (e.g, genetic sample of host species; geographic representation of spore populations used in the inoculum; environmental conditions affecting *Ribes* spp. growth rates; blister rust infection levels in the outdoor garden; spore load, length of exposure, and temperature and relative humidity in the indoor inoculation chamber). The spore load for the 110-seed source study (Mahalovich et al. 2006) was 3,695 spores/cm^2 and Cycle 1, a much 'hotter' load averaged 28,098/cm^2 to ensure identification of rust-resistant elite trees for the Little Bear Seed Orchard (Gallatin NF). Cycles 4 (2013-2017) and 5 (2014-2018) composed of seedlings from the remaining plus trees, will provide additional, rust resitsance measures for the GYE. A common checklot (universal bulk lot), families in common in Cycles 1-5, and modeling of inoculum and key environmental conditions in artificially inoculated whitebark pine seedlings, will provide an average estimate of expected gain with associated error variances to characterize rust resistance in the Northern Rockies and GYE and afford better comparisons among rust screening trials. Field monitoring of survivors planted in a performance test on the Gallatin NF, monitoring of planting units established with seedlings from known rust resistant locations and forthcoming, seedlings produced from seed collected at the Little Bear Seed Orchard, will provide measures of realized gain. Until data on realized gain becomes available, current rust-resistance levels guide silvicultural prescriptions to determine stocking levels (trees per acre) to achieve a desired future condition.

Figure 8. Blister rust resistance screening in five-needle pines at Coeur d'Alene Nursery, Coeur d'Alene, Idaho; red foliage is mortality due to blister rust. Photo credit D. Foushee.

Relative rust resistance

Blister rust resistance in the Northern Rockies is actually higher in whitebark pine (M. Mahalovich, U.S. Forest Service, unpublished data Cycles 16, 19-22) than western white pine (Bingham et al. 1960, 1969, 1972a, Hoff et al. 1980). One generation in a species is defined as two times the length of onset of reproduction, i.e., whitebark pine begins producing cones at age 20-30 years (Krugman and Jenkinson 1974), thus a conservative estimate of one generation is 60 years (30 years × 2). Whitebark pine has had 1.5 generations of natural selection to respond to blister rust, possessing 47.4% resistance in the Northern Rockies (Mahalovich et al.

2006). Contrasted to a similar exposure time, resistance in western white pine plus trees was determined to be 32.7% (Bingham et al. 1960, 1969, 1972a, 1972b, Hoff 1977). Within the GYE, whitebark pine has had 1.3 generations of natural selection to respond to blister rust, thus blister rust resistance (9-28%) was anticipated to be lower than western white pine.

Mountain pine beetle

Mountain pine beetle (*Dendroctonus ponderosae*) is a native insect that infests *Pinus* spp. and is currently causing widespread mortality in whitebark pine, lodgepole pine (*P. contorta* Douglas ex Loudon), limber pine, ponderosa pine *(P. ponderosa* Lawson and C. Lawson), and to a lesser extent, western white pine, southwestern white pine, and sugar pine. Mountain pine beetle is found as far south as Baja California Norte, Mexico and occur as far north as northern British Columbia and western Alberta (de la Giroday et al. 2012). Local and landscape factors influence the amount and distribution of tree mortality, resulting in a mosaic of undisturbed and beetle-killed forests (Larson and Kipfmueller 2012, Simard et al. 2012). Episodic outbreaks in recent history have occurred every 20-40 years (Raffa et al. 2008), covered extensive areas, with an average duration of 12-15 years. Historically, the typical life cycle of mountain pine beetle requires one year at lower elevations and two years at higher elevations. Development is highly dependent on temperature. Eggs are typically laid in late summer and larvae over-winter under the bark of susceptible pines (Figure 9). Feeding resumes in the spring and larvae transform into pupae as early as June and in to July. Adult beetles emerge from infested trees over the summer and early fall. The severity of current outbreaks in high elevation pines is attributed to warmer winters that have increased survival and warm summers that have allowed some proportion of broods to shift from a 2-year life cycle to a 1-year life cycle (Logan and Powell 2001, Logan et al. 2010, Bentz et al. 2011, Dooley 2012, Bentz et al. *in review*). Within the past decade, 47 million ha across all pine types in the Rocky Mountains have been impacted by mountain pine beetle (Raffa et al. 2008).

The USDA Forest Service annually performs aerial detection surveys (ADS) of forested lands to determine the approximate location and amount of tree mortality, defoliation, and other non-fire damaging agents (Box 2) (USDA Forest Service 1999). This type of survey is a landscape-level assessment of symptoms caused by insects, diseases, and abiotic factors, and in particular, damage caused by mountain pine beetle. The purpose of ADS is to map most forest change events that are new since the previous year's survey. ADS sketch maps have been recognized for over 50 years as an efficient and economical method of detecting and monitoring forest change events over large areas. This type of aerial survey is performed systematically so all areas of interest are adequately surveyed without large gaps of undocumented areas. Although large areas are covered, not all areas can be surveyed every year.

Box 2. Aerial Detection Surveys

Sketch mapping is a remote sensing technique of observing forest change events from a fixed-wing aircraft. The observer views a particular change event or damaged area and manually delineates the affected area onto a map to record its size, shape, and location. Attributes such as host, causal agent, symptom, and an estimate of intensity or number of trees affected are recorded. Since it is a relatively low cost method, it is relied upon to provide a coarse, landscape-level overview of forest health conditions. If the forest change events discovered during the overview survey are considered a high priority, it can be used as the first step of a multi-tiered process of detection, monitoring, and evaluation using other remote sensing and ground-sampling techniques.

There is considerable annual variation in ADS data because of the amount and specific areas surveyed. Acreage data include both whitebark and limber pine mortality because of the difficulty of discerning the two species from the air. Geospatial data and metadata of recent aerial detection surveys are available at http://www.fs.usda.gov/detail/r1/forest-grasslandhealth/?cid=stelprdb5

Figure 9. Mountain pine beetle larvae and pupae in whitebark pine. Photo credit S.J. Kegley.

Mountain pine beetle in the GYE

The first reported outbreak of mountain pine beetle in whitebark pine began around 1925 (Furniss and Renkin 2003), a pattern seen across much of the western US (Perkins and Swetnam 1996, Margoles 2011). The majority of mature whitebark pine was infested by 1937, and by 1942, mountain pine beetle was no longer considered a problem (Despain 1990). The next major epidemic occurred from 1969 to 1985, characterized by two, overlapping outbreaks with 1980 attributed as the peak year (USDA

Forest Service 2012a, 2012b, 2012c, Olliff et al. 2013). The most recent outbreak of mountain pine beetle in the GYE began in 1999-2000 (Figure 10). Macfarlane et al. (2010, 2013) using Landscape Assessment System found over 50% of whitebark pine stands in the GYE exhibited high levels of mortality in overstory trees, and 95% of these stands had detectable levels of mountain pine beetle activity.

Peak beetle activity occurred in 2009 (215,150 ha of 6,398,020 ha flown, Figure 11) (USDA Forest Service 2012a, 2012b, 2012c). Aerial detection surveys indicate the outbreak is waning (Figure 11) with the expectation of occasional 'blow-outs' at smaller scales over the next 3-8 years (G. DeNitto, personal communication). Based on the annual decline in the number of acres damaged since 2009 (Figure 11), there is no indication of a possible back-to-back outbreak.

Figure 10. Greater Yellowstone Area Ecoflight in 2009 during the peak of the most recent mountain pine beetle outbreak. Photo credit J. Pargiter.

Figure 11. Annual mountain pine beetle damage (2000-2012) from USDA Forest Service aerial detection survey in whitebark and limber pines in the Greater Yellowstone Ecosystem (USDA Forest Service 2012a, 2012b, 2012c, GIS support courtesy K. Mathews).

The USDA Forest Service aerial detection surveys indicate 598,875 ha of 1 million ha (1,479,853 of 2,528,322 ac) of cumulative mapped damage (Figure 12), or 58.5% of dominant and mixed stands of whitebark pine in the GYE, have been impacted as of 2012 (USDA 2012a, 2012b, 2012c). Acres reported to mountain pine beetle damage indicate the upper bounds of *all* five-needle pine damage (i.e., whitebark and limber pine). The following caveats to acres reported are as follows: 1) the Northern Region (R1) stopped separating host species mountain pine beetle damage in 2007 and acre totals from 2007-2012 include both limber pine and whitebark pine; 2) the Rocky Mountain Region (R2) converted assessments to a five-needle pine causal agent in 2002 and acre totals from 2002-2012 include both limber and whitebark pine; and 3) the Intermountain Region (R4) data from 2002-2012 are specific to whitebark pine.

Among the aforementioned 76 sampled locations representing 2,610 ha in the whitebark pine genetics program, the incidence of mountain pine beetle from 2001, 2003-2012 is 0 to 98% ($\bar{x}$ = 20.4%, ±27.7) with the highest incidence in the northwestern section of the GYE (Figure 13) (M. Mahalovich, U.S. Forest Service, unpublished data).

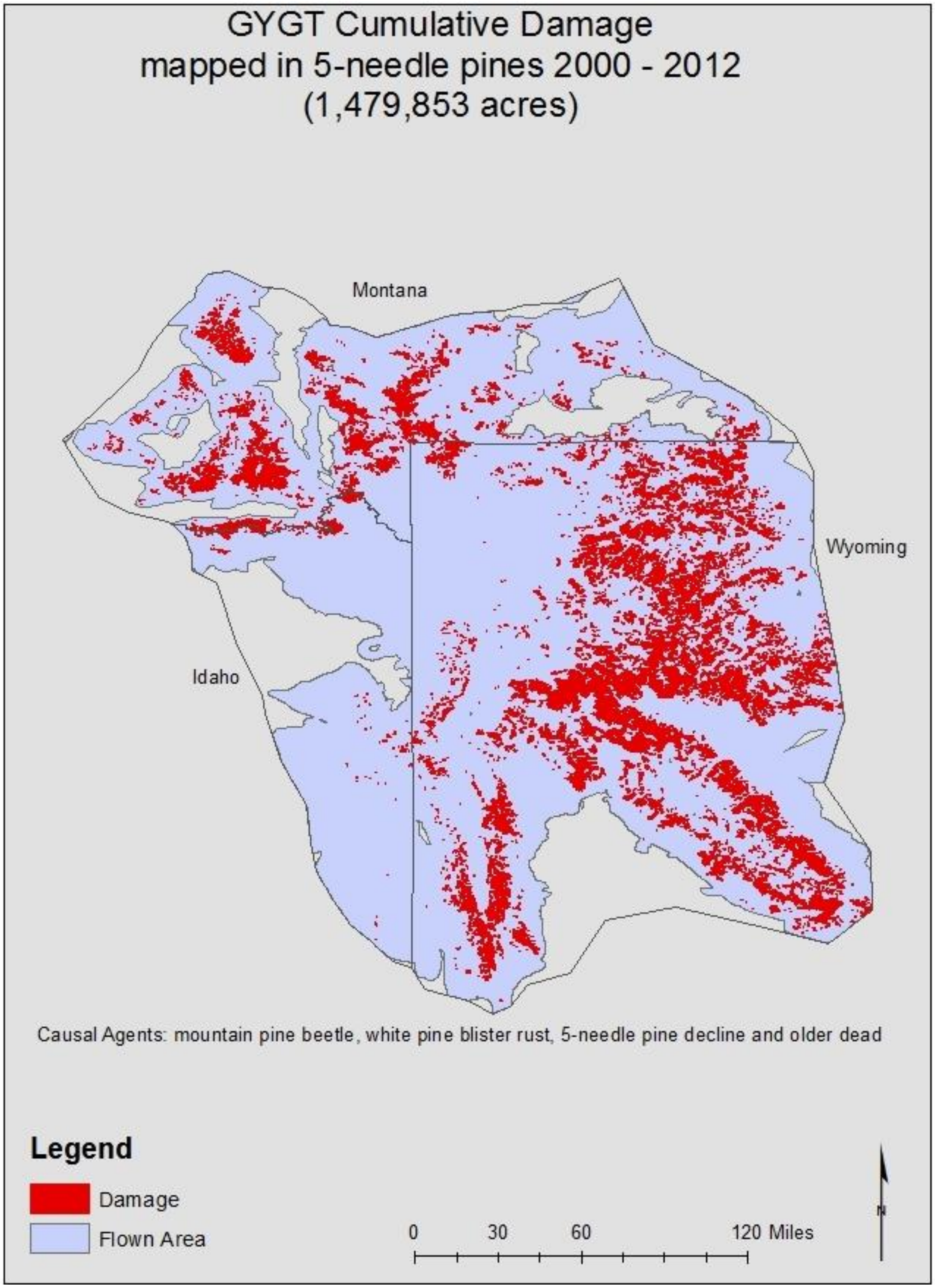

Figure 12. Cumulative mountain pine beetle, blister rust, and older dead damage in whitebark and limber pines in the GYE from USDA Forest Service aerial detection surveys (2000-2012).

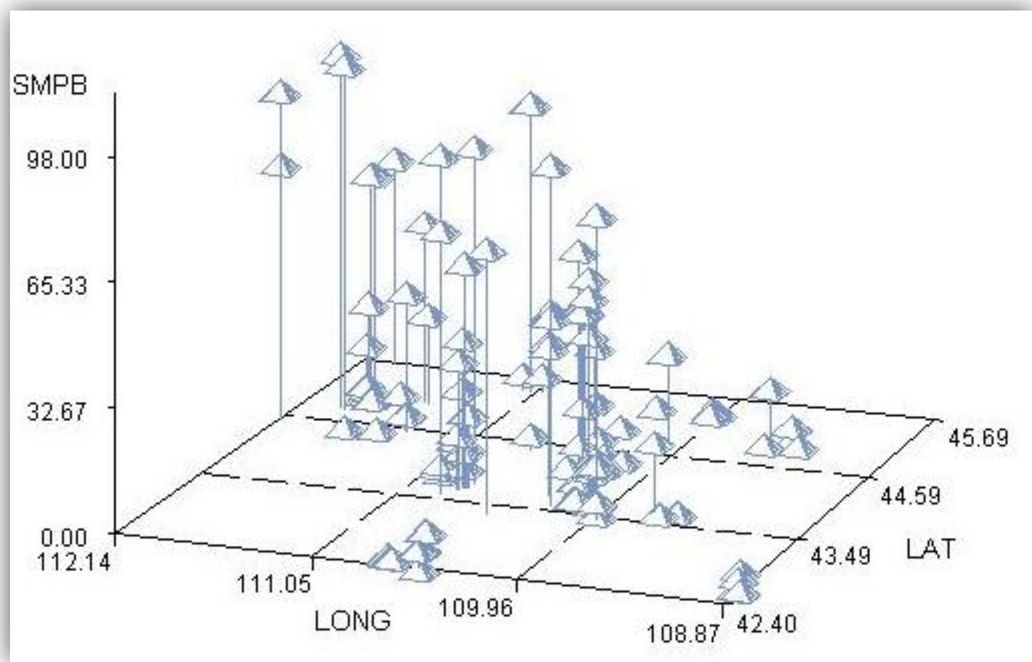

Figure 13. Mountain pine beetle infestation levels (SMPB) among 76 geographic areas represented in the GYE whitebark pine genetic restoration program 2001, 2003-2012 (M. Mahalovich, U.S. Forest Service, unpublished data).

Other factors impacting whitebark pine

Concerns of correlated response in whitebark pine, particularly an unfavorable interaction between blister rust infection and mountain pine beetle incidence levels, have been put forth by Six and Adams (2007), Bockino and Tinker (2012) and Dooley (2012). Host selection ratios developed by Macfarlane et al. (2010, 2013) assume trees with more blister rust infection are prone to mountain pine beetle attacks. Schwandt and Kegley (2004) found that mountain pine beetle preferred trees infected with blister rust in north Idaho when beetle populations were low; however, during epidemics, beetles preferentially attacked trees with little or no blister rust. Dooley (2012) hypothesized that mountain pine beetle tree selection is nonlinear and increased with blister rust infection levels only to a point, after which it decreased.

Correlated response

Between two traits, correlated response from a genetics perspective has a basis in linked genetic loci, overlapping genetic loci, or both. Plus trees in the genetics program provide a biological basis for testing the hypothesis that there are one or more unfavorable, correlated responses among traits. When it is difficult to estimate a genetic correlation (r_A) and test its significance, r_A can be replaced with a correlation among family means, i.e., as the number of measured individuals for a family increases, the sampling error of the mean becomes so small that the phenotypic mean is approximately equal to a genetic mean. Pearson mean correlations among the plus trees do not indicate an unfavorable correlation between blister rust infection and high mountain pine beetle outbreaks, whether those data are pooled across years or analyzed by year. Blister rust infection is weakly correlated with mountain pine beetle incidence ($r = 0.01$, $p < 0.88$), as is average canker count ($r = 0.03$, $p < 0.67$) (M. Mahalovich, U.S. Forest Service, unpublished data). Blister rust was first identified in the GYE in 1937, so within the recent evolutionary history (1.3 generations), this timeframe is not long enough for whitebark pine to have established a correlated response between an introduced pathogen and an endemic insect. Moreover, blister rust infection, number of cankers, and mountain pine beetle incidence are weakly related geographically, increasing with latitude and longitude and decreasing with elevation.

Mahalovich et al. (2006) and Mahalovich (*in prep*) evaluated correlated response among blister rust resistance, survival, late winter cold hardiness, and early growth. Rust resistance as described by seven traits was weakly correlated with 6^{th} year height, where seed sources from northwestern locations were taller and have more rust resistance ($r = 0.14$). Rust resistance was weakly correlated ($r = 0.27$) to cold hardiness, where populations from lower elevations or geographically milder sites were more resistant but had low freezing tolerance. Survival was moderately correlated to cold hardiness ($r = 0.45$) and 6^{th} year height (r=0.36). Seed sources from lower elevations or geographically milder sites were taller but had low freezing tolerance. Collectively, small and non-significant correlations and weak geographic gradients suggest unfavorable, correlated response among traits is of little concern.

Cone production, masting patterns, and natural regeneration

Reduced tree densities due to mortality from mountain pine beetle, blister rust, wildland fire, and stand isolation has the capacity to reduce seed cone maturity and impact masting patterns (Rapp et al. 2013). Pease and Mattson (1999) characterized mast years as >20 cones per tree. McKinney et al. (2009) report a threshold of 1,000 cones per ha (2.47 ac) are needed to ensure seed dispersal by Clark's nutcrackers (*Nucifraga columbiana*). This threshold equates to 25-50 cone bearing trees per ha (10-20 cone-bearing trees per ac). From an effective pollination cloud to provide adequate pollination of receptive ovules, a minimum of 25 reproductively mature *Pinus* spp. per ha are required. Furthermore, for wind-pollinated conifers, 50-125 reproductively mature trees per ha ensure a genetically diverse cone crop with minimal consequences of inbreeding depression. Inbreeding depression in the progeny population is defined as an immediate reduction in germination, high early mortality in seedlings, and in saplings that do survive to maturity, poor growth and loss in fecundity.

Stocking surveys of natural regeneration are an indirect method to assess the effectiveness of tree density and cone production in whitebark pine. A mixture of seedling and sapling whitebark pine natural regeneration is present throughout western North America, varying from as few as 72 trees per ha on the Flathead NF, 506 trees per ha on the Bridger-Teton NF, 1,630 trees per ha on the Gallatin NF (M. Mahalovich, U.S. Forest Service, unpublished data 2012), to as many as 7,000 trees per ha in southwestern Montana, central Idaho and Oregon (Larson and Kipfmueller 2010). Tree ages were determined by counting whorls where the majority of the recruitment was in the 20-40 year age class, indicating regeneration since the 1970s and 1980s mountain pine beetle outbreak. Trees in the central Idaho seed zones (Bitterroot and Payette NFs) were approximately 5-7 feet tall bearing 5-9 cones per tree in the upper third of the crown. At the Cooke City site on the Gallatin NF, two to three-year old clumps of seedlings were also noted, indicating recruitment since the 2009 masting event.

While warmer temperatures facilitate seed germination, mortality among seedlings can be high due to heat scorch and drought. Therefore, seedlings on cooler sites will likely have higher sapling recruitment rates (McCaughey et al. 2009). Warmer temperatures and droughty conditions projected in the GYE carries a higher likelihood of limiting natural regeneration following masting events. Although warmer temperatures and drought may initially limit whitebark pine natural regeneration, those surviving seedlings and saplings will have a higher likelihood of reaching maturity, due to unfavorable climatic conditions that limit alternate host regeneration and disruption of the blister rust infection cycle.

Climate Change

Projected increases of atmospheric CO_2 and subsequent changes in temperature and precipitation patterns have the potential to alter ecosystem function, species interactions, population biology, species distributions and plant assemblages (Melillo et al. 1990, Kirschbaum 2000, Iverson et al. 2008). Increases in temperature will lead to shifts in disturbance regimes such as fire and insect outbreaks (Kipfmueller 2007). General trends in vegetation in the western United States in response to climate change indicate species range shifts north in latitude and up in elevation (McKenney et al. 2007, Aitken et al. 2008).

Early approaches of climate change projections involve bioclimatic envelope modeling emphasizing the presence or absence of an individual species' geographical distribution (Little 1971) at the 1-km^2 grid scale. Climatic data is simulated using Hutchinson's thin plate spline approach (Rehfeldt et al. 2006, 2012). Modeling outcomes focus on extinctions and the notion that species migration without human intervention will not be able to keep up with abrupt climate change (Aitken et al. 2008, Wang et al. 2012). More recent approaches have transitioned to niche modeling, where all life stages are considered (e.g., seed dispersal, germination, and ecesis, Appendix I). Similarly, the accuracy of projected distributions for whitebark pine will be determined by climate models that incorporate geophysical properties, inter-species competition, host-pathogen interactions, and phenotypic plasticity.

Whitebark pine decline

Whitebark pine is declining across most of its range. Since it is a long-lived species and grows near the physiological limit of tree growth, variations in ring-widths are sensitive to changes in climate. Kipfmueller (2007) attributed a shift from temperature as a primary factor limiting growth to a more mixed signal, whereby moisture conditions may be more limiting as a result of rising temperatures during the course of the 20th century. From the perspective of disturbance agents, stands in the mesic, warmer portions of its range are experiencing mortality due to blister rust and mountain pine beetle (Kendall and Keane 2001, Gibson et al. 2008, Kegley et al. 2011, USDA Forest Service 2012a, 2012b, 2012c). Even the driest, coldest parts of the species range are experiencing blister rust infections (Bockino 2008, Resler and Tomback 2008) and beetle mortality (GYWPMWG 2012, 2013, USDA Forest Service 2012a, 2012b, 2012c). Whereas the GYE has historically had the lowest blister rust infection and mountain pine beetle outbreaks, recent increases in blister rust and extensive beetle mortality are contributing to major declines of whitebark pine (Jewett 2009; Hicke and Logan 2009; Hatala et al. 2011, GYWPMWG 2012, Rice et al. 2012, USDA Forest Service 2012a, 2012b, 2012c).

Hypotheses of the impacts of increased temperatures threatening whitebark pine indicates potential habitat shifting upslope, moving its lowest elevation occurrence above tree line (Romme and Turner 1991, Bartlein et al. 1997, Warwell et al. 2007, Schrag et al. 2008, Millar et al. 2012). In its wake, more shade tolerant conifers (*Abies lasiocarpa* (Hook.) Nutt., *Picea engelmannii* Parry ex Engelm., and *Pseudotsuga menziesii (Mirb.) Franco*) would be able to establish at higher elevations where whitebark pine currently dominates (Koteen 2002). Projections through 2030 indicate a widespread decline in the presence of whitebark pine (Warwell et al. 2007, McDermid and Smith 2008), with <3% of currently suitable habitat expected to remain by 2100 (Warwell et al. 2007). For the Glacier NP ecosystem, Loehman et al. (2011) indicated a more favorable outlook for whitebark pine if large, stand-replacement fires create competition-free burned areas for natural regeneration or if site preparation occurs for restoration planting.

Blister rust and its alternate hosts

Weather variables that affect the spread and intensity of blister rust are temperature, precipitation, relative humidity, and wind (Fujioka 1992). A warmer climate may accelerate the spread of blister rust (Koteen 2002), particularly at higher elevations (Larson 2011). Then as blister rust intensifies within a location, these areas typically give rise to some of the more rust-resistant pine (Bingham 1983). From an intense artificial inoculation and blister rust screening of whitebark pine progeny (2008-2013), seedlings from plus trees from within the GYE originating in high rust infection areas are positively correlated with increased blister rust resistance (r= 0.21, p<0.0001) (i.e., blister rust is weeding out the more rust-susceptible genotypes) (M.Mahalovich, U.S. Forest Service, unpublished data). Geographic patterns of rust resistance are similar to projected rust infection levels found in Figure 4. Blister rust resistance among these seedlings increase with increasing latitude and longitude, decreasing elevation, decreasing aspect, increasing frost-free period , decreasing late spring thaw (or the sum of the number of degrees days to reach 100°C), and decreasing summer-spring precipitation balance. A physiological explanation for this relationship is that as the frost-free period occurs earlier and lasts longer, whitebark pine has the capacity to break bud and complete a season of growth earlier. Then soon after spring thaw and peak growth, whitebark pine can set its terminal and lateral buds earlier in the growing season. As a result of this plasticity, the needle tissue is no longer actively growing and is thereby less susceptible to infection from blister rust later in the season. When container-grown western white pine seedlings have been hardened-off by applying finishing fertilizers (lower N and higher P and K) and withholding irrigation at the end of the growing season, these seedlings are more difficult to infect with blister rust (A. Eramian, personal communication).

Rising temperatures and decreased or variable precipitation slows the spread of blister rust under more arid conditions (Geils et al. 2010). Sturrock et al. (2011) categorized blister rust by temperature and moisture relative to rust reproduction, spread, infection, and survival, whereby blister rust is predicted to decrease in impact in warmer and drier future climates or to have no change in impact with warmer and wetter climates. Aeciospore germination is restricted when spores are exposed to temperatures exceeding 36°C, urediniospore production is limited when temperatures exceed 35°C and prevented altogether by 10 days of exposure at higher temperatures, and teliospore production is inhibited by three consecutive days above 28°C (Van Arsdel et al. 2006). Basidiospore viability and germination is inhibited by extremes of drying and wetting, temperatures exceeding 21°C and lethal above 35°C, exposure to direct light, and sustained low humidity (Van Arsdel et al. 2006). Thus, decreasing relative humidity and higher temperatures in late August and September will impede basidiospore development, transport, and germination in whitebark pine. Alternatively, mesoscale weather systems such as late summer thunderstorms can interrupt arid conditions and temporarily produce the cool, moist conditions favored by basidiospores for germination and host infection (Fujioka 1992).

Rising temperatures will also impact the alternate host species. Earlier thaws and later fall frosts will increase the growing season for *Ribes* spp.. *Ribes* spp. are usually early-serals, often thriving under high light conditions and reduced competition. Following a fire, *Ribes* spp. quickly re-colonize a site vegetatively, by sprouting from the root crown or by germinating from seed stored in the local soil bank (Van Arsdel et al. 2006, Zambino 2010). As the overstory develops, the relative abundance of each species declines according to its shade intolerance and with succession, some *Ribes* spp. are outcompeted in the understory. Warmer and drier climatic conditions may thus favor these early seral species.

Like its pine host, susceptibility is defined as the capacity of *Ribes* spp. to become infected and support inoculum production. Susceptibility varies by plant (e.g., leaf age, shading, leaf temperature, and wetness), local environment, exposure to different strains of rust, and even by how it is assessed in the field vs. a controlled environment (Zambino and McDonald 2004, Van Arsdel et al. 2006). Increasing rates of blister rust infections will be tempered by stocking in suitable habitat of the more susceptible (gooseberry current *R. montigenum* McClatchie, prickly current *R. lacustre* (Pers.) Poir., and sticky current *R. viscosissimum* Pursh) or less susceptible (wax current *R. cereum* Douglas) *Ribes* spp. to blister rust infection (Van Arsdel et al. 2006, Table 2).

The ecological roles of *Pedicularis* and *Castilleja* in the life cycle of blister rust and changing climate may range from critically important to insignificant, depending on the ecosystem and local pine host phenology, and the proximity of pine hosts to blister rust (Zambino 2010). These alternate hosts are more prevalent than *Ribes* spp. in high-elevation ecosystems and are speculated to have a greater impact on blister rust in whitebark pine (Richardson et al. 2007). Both current and future impacts of these alternate hosts relative to whitebark pine are poorly understood.

As the life cycle progresses among alternate hosts, increased temperatures, lower relative humidity, and variable precipitation in late August and September, will most likely disrupt the exacting conditions necessary for infection of the alternate host species and whitebark pine (Van Arsdel et al. 1956, Van Arsdel 1967, Kliejunas et al. 2009). Future increases in blister rust infection levels may be limited to infections during wave years. Kinloch (2003) anticipated that as climates become warmer and drier, weather conditions favoring wave years will diminish. Our ability to predict wave years will require stratifying precipitation and temperature conditions that correlate with intensified rust activity and mesoscale meteorological modeling to characterize long-distance jumps in blister rust (Fujioka 1992). Lastly, ornamental releases of alternate hosts also have the potential to spread blister rust into native flora, however, their impact is likely to be limited. Although blister rust is widespread throughout North America, the role of fire, climate change, relative susceptibility in the alternate hosts, coupled with the exacting conditions needed for spore development and germination, guarantees a highly unpredictable outlook for blister rust.

Mountain pine beetle

Bark beetles have the capacity to respond to climate changes faster than their host species (Bentz et al. 2005, 2010). Eggs and pupae are most susceptible to freezing temperatures. Winter temperatures from as few as several straight days to as many as 40 days below -40°C are reported necessary to naturally kill off large portions of mountain pine beetle populations, depending on the timing of low temperature relative to the acclimation process of the insect. Temperatures below -35°C are also effective in killing off mountain pine beetles, before snow accumulation provides insulation to overwintering larvae. In the early fall or late spring, sustained temperatures of -25°C may result in beetle mortality. Sudden cold snaps are more lethal in the fall before beetles are able to build up their natural anti-freeze (glycerol) levels (Sømme 1964, Bentz and Mullins 1999).

Aukema et al. (2008) found the presence of outbreaking mountain pine beetle populations in British Columbia during the 1970s and 1980s was highly correlated with outbreaking populations within the nearest 18 km the same year and local populations within 6 km in the previous two years, with increasing temperatures contributing to outbreak probabilities during this 15-year outbreak. Other field studies and general observations in British Columbia show that once mountain pine beetles infest a stand, they kill between 50-100 percent of large, mature cone-bearing whitebark pine within 1-4 years (Campbell et al. 2011). Warm winter temperatures increase survival and warm summers allow a shift in some proportion of high elevation populations from a 2-year to a 1-year life cycle (Logan and Bentz 1999, Logan and Powell 2001, Logan et al. 2003; Campbell et al. 2011, Preisler et al. 2012, Bentz et al. *in review*). Recent increases in winter and summer temperatures have contributed to increased mountain pine beetle caused mortality at higher elevations, as well as in lower elevation pine ecosystems.

Perkins and Roberts (2003) using logistic regression found tree diameter, basal area per 0.04 ha, trees per 0.04 ha, and number of stems in a tree cluster were significant predictors of individual tree attack ($p \leq 0.001$). Similarly, plot-level measures (stand structure and soil characteristics) though weak, were better at predicting mountain pine beetle severity in the GYE (R^2_{adj} – 0.25, $p = 0.0287$) than models including a landscape context and beetle pressure (Simard et al. 2012).

Pinus spp. hosts extend beyond the range of mountain pine beetle to the north and south, indicating that this species is currently limited by climate rather than host availability. Within the past decade, mountain pine beetle has expanded its range north into northern British

Columbia and western Alberta (de la Giroday et al. 2012). Population activity has also increased in high elevation forests (Gibson et al. 2008). Temperature-dependent evolved adaptations predict that cool habitats are where mountain pine beetle is most able to take advantage of warming temperatures (Bentz et al. *in review*). Future bark beetle outbreaks may shift north in latitude and up in elevation (Amman 1973), be highly variable both spatially and temporally (Aukema et al. 2008), and further increases in temperature may result in forest ecosystem shifts beyond historical bounds (Bentz et al. 2010).

Climate change in the GYE

The GYE is divided into two climatic regions (Whitlock and Bartlein 1993, Curtis and Grimes 2004, Rice et al. 2012). The west and northwest portion of the ecosystem is characterized by wet winters and dry summers and the reverse relationship (dry winters and wet summers) in the east and southeast (Wilmers et al. 2013). Jewett (2009) and Jewett et al. (2011) found the highest mortality in whitebark pine on warmer, drier sites in the GYE, whereby this relationship was likely mediated by mountain pine beetle. Higher elevation habitats of whitebark pine are experiencing more rapid increase in temperature than lower elevations (A. Rodman, personal communication). Warmer temperatures relative to mountain pine beetle outbreaks, drought stress, alternate host species' growth, and the exacting conditions needed for rust infection, may mitigate future increases in rust infection levels or expansion into areas with low rust pressure, i.e., higher rust infections in whitebark pine will likely shift from the west and northwest portion of the GYE to the east and southeast. Blister rust expansion has been proceeding into the GYE from the NW to SE direction; thus, climate change will likely facilitate the rate at which it proceeds.

How generalists fare in changing climates

A species' adaptation to heterogeneous environments was first considered by Mather (1943) as a compromise between fitness for current conditions and a species' flexibility for accommodating changed conditions. Levins (1968) established the protocol for characterizing how a species achieves adaptation to heterogeneous environments. Population differentiation tied to abiotic (e.g., edaphic) conditions can be rare.

Rehfeldt (1994) characterized the genetic structure of conifer species with different evolutionary strategies as a specialist, intermediate, or generalist. Another way to characterize a species' adaptive strategy is by partitioning patterns of genetic variation in adaptive traits, whereby populations are tested alongside one another in a common garden study (Table 2). Species that are grouped into numerous local populations that are physiologically, biologically or abiotically attuned to a narrow range of environments are classified as specialists (*Pinus contorta* (Rehfeldt 1988, 1999), *Pseudostuga menziesii* (Rehfeldt 1974, 1989, 1990)). The intermediate adaptive strategy is characterized as populations suited to a broader range of environments, but showing some differentiation to local habitats or climes (*Pinus ponderosa* (Rehfeldt 1991), *Larix occidentalis* (Rehfeldt 1992, 1995a, 1995b)). Lastly, a species exhibits a generalist adaptive strategy if populations are physiologically, biologically or abiotically attuned to a broad range of environments (*Pinus albicaulis* (Mahalovich *in prep*), *P. monticola* (Rehfeldt 1979, Rehfeldt et al. 1984).

Species that are range-restricted, are located at the margins of climate tolerance, have slow reproduction rates, or have narrow environmental tolerance are projected to be the most sensitive to climate change and experience the largest range contractions, population reductions, and extinctions (Parmesan 2006, Ohlemuller et al. 2008). Because of its long life span (500-1,200 years) (Perkins and Swetnam 1996), whitebark pine may be a species that is unable to adjust to rapid climate change. Long-lived tree species however, typically have high levels of genetic diversity (reviewed in Mahalovich and Hipkins 2011) and in the case of tree species exhibiting a generalist adaptive strategy, also have the capacity to adjust to rapid climate change via phenotypic plasticity (Table 2).

Table 2. Comparison of attributes characterizing a species' adaptive strategy.[1]

	Adaptive Strategy	
Attributes	Specialist	Generalist
Factor controlling phenotypic expression of adaptive traits	Genotype	Environment
Mechanisms for accommodating environmental heterogeneity	Genetic variation	Phenotypic plasticity
Range of environments where physiological processes function optimally	Small	Large
Slope of clines for adaptive traits	Steep	Flat
Partitioning of genetic variation in adaptive traits	Among populations	Within populations

[1] Modified after Rehfeldt (1994).

Although whitebark pine in the Northern Rockies is geographically widespread across a range of 2,000 m in elevation, the near absence of systematic differentiation among populations, with the majority of population differentiation present at landscape-level scales, indicates a species with a generalist adaptive strategy. Thus, high levels of genetic diversity (Mahalovich and Hipkins 2011, Richardson et al. 2002), moderate to high heritabilities in key adaptive traits (Mahalovich et al. 2006, Mahalovich *in prep*), demonstrated blister rust resistance (Mahalovich et al. 2006, M. Mahalovich, U.S. Forest Service unpublished data), minimal inbreeding

(Mahalovich and Hipkins 2011), and a generalist adaptive strategy (Mahalovich *in prep*), indicates whitebark pine shows promise for being maintained in the GYE.

Conclusions

The U.S. Fish and Wildlife Service's working definition of functionally extinct refers to a few live adults that do not appear to be reproducing in order to sustain the population as a whole (USFWS 2013, B. Walling, personal communication). From the perspective of a food resource, 'functionally extinct' would refer to a food source no longer available in meaningful quantities to grizzly bears (C. Servheen, personal communication). Conservation biologists define a species as functionally extinct if it has: 1) disappeared from the fossil record, 2) occurs in isolated, disjunct populations with low population numbers, 3) has high inbreeding and low fecundity, and 4) exhibits local extirpation of populations (Holdaway 1999, Luck et al. 2003). Although whitebark pine has experienced widespread decline (Keane et al. 2012), it is still very much on the landscape and thus has not disappeared from the fossil record (Table 3). Whitebark pine naturally occurs in isolated, disjunct populations in high elevations in part due to its coevolution with Clark's nutcracker (Tomback 2005) and its ability to thrive in harsh, windswept sites. Annual seed extraction reports (USDA Forest Service 2012) and IGBST permanent cone transect surveys (Haroldson and Podruzny 2013) indicate whitebark pine is reproducing in the wild. The degree to which blister rust, mountain pine beetle, wildland fire, and fire suppression exacerbates isolated, disjunct populations will ultimately depend on the density of healthy, reproductively mature whitebark pine per (>20 per ha). Whitebark pine in the Northern Rockies and specifically the GYE, exhibits no inbreeding (9.354 migrants per generation and an outcrossing rate of 0.98, with 1 being the maximum) (Mahalovich and Hipkins 2011). Due to masting events and recent stocking surveys of natural regeneration, it currently is not exhibiting low fecundity; there is a temporal component to the species distribution as whitebark pine populations rebuild following mountain pine beetle outbreaks. Localized populations of western white pine have been lost to blister rust, and lodgepole pine and Ponderosa pine populations have been lost due to endemic diseases. All have experienced mountain pine beetle outbreaks and wildland fire, however, these pines are not considered functionally extinct.

Ensuring a functioning regeneration cycle is critical to retain and promote the resiliency and adaptation of whitebark pine in the GYE. Restoration planting and natural regeneration play vital roles in support of the regeneration cycle (Keane et al. 2012). Fostering natural regeneration will increase both the number of new genetic combinations and frequency of adapted-gene complexes.

Increasing the frequency of rust resistance before rust-infection levels intensify supports the regeneration cycle, whereby resistant trees mature before the existing cone-bearing trees die (Schoettle et al. 2009). Adequate stocking of reproductively-mature whitebark pine promotes pollination and fertilization to produce the next generation of whitebark pine, while minimizing the negative consequences of inbreeding depression or mating among relatives.

Table 3. Spatial measures[1] of biological stress and genetic health characterizing the ability of whitebark pine to respond to evolutionary forces *in situ* or through genetic improvement.

Genetic Hierarchy	Blister Rust Infection	Blister Rust Resistance	Rust Resistance Family Heritability	Mountain Pine Beetle Incidence	*He* expected hetero-zygosity
Species	0-100%	41-47%	0.68 (n=110)	0-100%	0.271
Landscape or region (GYE)	20-37%	28% (n=19) 9% (n=113)	0.70 (n=19) 0.72 (n=113)	0-100%	0.254
Population, stand or area	0-100%	--	--	0-100%	--
Family	52-89% (n=19) 33-100% (n=113)	11-48% (n=19) 0-64% (n=113)	--	--	--
Individual-tree	Presence or absence	Presence of no-spot, needle shed, short shoot, bark reaction, or canker tolerance traits	--	Presence (low, medium or high number of hits) or absence	--

[1] n=19 Greater Yellowstone Ecosystem (GYE) 110-seed source study (Mahalovich et al. 2006)
n=113 GYE Cycle 1 blister rust screening (M. Mahalovich, U.S. Forest Service, unpublished data)

Federal agencies in the Whitebark Pine Subcommittee of the Greater Yellowstone Coordinating Committee also have access to blister rust resistant seedlings for restoration planting (Mahalovich and Dickerson 2004, Mahalovich et al. 2006, Schwandt 2006, Schwandt et al. 2010). Recent planting accomplishments from 2000-2013 average 102 ha per year (Figure 14). The Greater Yellowstone Area Strategy supports planting 365 ha per year (GYCCWBPS 2011).

Lastly, an examination of the history of western white pine will provide another indication of what we can expect for the future of whitebark pine (Fins et al. 2001). Western white pine is under siege from all of the same threats as whitebark pine (e.g., blister rust, mountain pine beetle, altered fire regimes, and climate change). By the late 1990s, the distribution of western white pine had been reduced to 5-10% of the original 2 million ha of white pine cover type in the Inland Northwest (Fins et al. 2001). An aggressive breeding program to accelerate natural variation in blister rust resistance has provided an outlet for blister rust resistant seedlings from production orchards (Mahalovich 2010). Since 1978, approximately 74,390 ha have been planted with blister rust resistant seedlings (Mahalovich 2010, M. Rust, Inland Empire Tree Improvement Cooperative, unpublished data). Recent planting efforts average 405 ha per year. A newer assessment of the species' distribution would indicate whether the combined efforts of reforestation and natural regeneration have contributed to an increase of western white pine cover type in the Inland Northwest. Relying exclusively on natural processes to restore western white pine to its former ecological position will be slow and uncertain at best, especially in areas where only a few remnants remain to provide a seed source (Fins et al. 2001).

The prognosis for whitebark pine is nothing better than its current distribution, and in the absence of a breeding program to advance rust resistance, paired with more planting or direct-seeding (McLane and Aitken 2012, McLane 2011), perhaps something less. How much 'less' will be a function of blister rust infection levels, future outbreaks of mountain pine beetle, wildland fire, fire suppression, species competition at lower elevations, regeneration losses due to drought, and as species move north or upslope, regeneration losses due to cold hardiness.

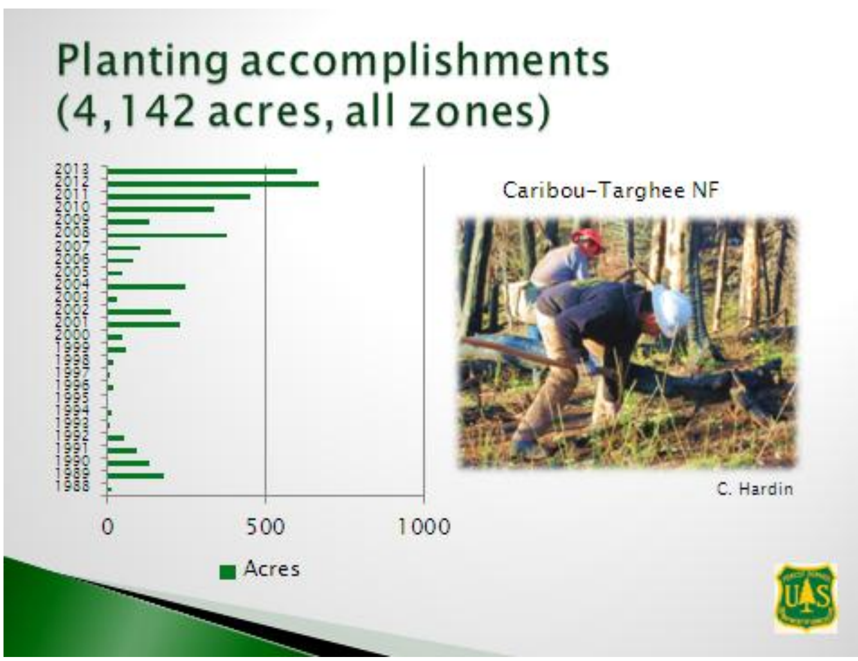

Figure 14. Approximately 1,676 ha (4,142 ac) from 1991 to 2013 have been planted to whitebark pine in the Northern Rockies, with approximately 70% occurring within the GYE (USDA Forest Service 2013).

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Appendix I. On-going climate change research in the GYE

Title: Modeling ecosystem processes and system types to forecast for climate change (Using NASA Resources to Inform Climate and Land Use Adaptation)
Collaborators: Andy Hanson (Montana State University) Tel: (406) 994-6046 E-mail: hansen@ montana.edu , Tom Oliff (NPS, Great Northern Landscape Cooperative) (406) 994-7920; tom_olliff@nps.gov , Bill Monahan (NPS Fort Collins, CO), Scott Goetz, Forrest Melton, Ramakrishna Nemani, David Theobald, and John Gross. Project funded by NASA.
Objectives:

a. Predict changes in whitebark pine ecosystems over time using only climate variables – if beetles, rust, fire regimes, competition were removed from the equation, what effect would climate alone have?
b. Create a climate and habitat suitability model for survival, growth, and reproduction – not just species presence / absence. Life stage and habitat factors have not been selected as of April 24, 2012. Olif reported life stages selected and modeling completed (natural regeneration, cone-bearing trees, etc.) May 14, 2013, but not available on web or peer-reviewed publications.
c. Predict changes in suitable planting areas – different latitudes and elevations may become hospitable to whitebark pine over time.
d. Develop management recommendations based on climate projections (could influence planting locations).

Products: (1) climate, productivity, runoff datasets, (2) synthesis of primary research, (3) Down-scaled climate projections, (4) provide stronger justification for management actions/NEPA http://www.montana.edu/lccvp/index.html
Time frame: 4-year project in its 1st year (2012) through July 2015

Title: Climate change indicators, what are they really telling us?

Collaborators: Ann Rodman (YNP) Mike Tercek, Sonoran Institute, Phoenix, AZ mtercek@sonoraninstitute.org (406) 329-4846, David Thoma, Allison Klein

Objectives: Define appropriate climate change indicators for GYE (suggested EPA indicators a starting point). Using four climate stations within the GYE (Mammoth, Moran, Lamar, Cody, Gardiner, Tower, Parker Peak) how fast are the maximum and minimum temperatures changing.

Products: http://www.yellowstoneecology.com/research/research.html . Note projects is not specific to whitebark pine. Preliminary report at GYCC Whitebark pine subcommittee meeting May 14, minimum temperature is changing faster. Presented phase shift concepts where climatic extremes prior to 1990s are now within 1 SD of the climatic normal.

Tercek, M.T., S. Gray, and C. Nicholson. 2012. Climate Zone Delineation: Evaluating approaches for use in natural resource management. Environmental Management. DOI: 10.1007/s00267-012-9827-4

Time frame: Ongoing

Title: RMRS

Collaborators: Bob Keane rkeane@fs.fed.us (406) 329-4846. Rachel A. Loehman, Allisa Corrow. **Objectives:** Simulate what is going to happen with WBP based on disturbance (fire, MPB) using A2 and B2 climate models with and w/o planting. Focus areas Glacier, Bob Marhsal and East Fork of the Bitterroot. No GYE component.

Products: Glacier version published. Bob Marshall and East Fork of Bitterroot on-going.

Loehman, Rachel A.; Corrow, Allissa; Keane, Robert E. 2011. Modeling climate changes and wildfire interactions: Effects on whitebark pine (*Pinus albicaulis*) and implications for restoration, Glacier National Park, Montana, USA. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 176-189. Landscape simulation modeling will be used to develop detailed management guidelines for restoring and sustaining whitebark pine under future climates, accounting for the principal stressors that threaten its persistence (exotic disease infections, mountain pine beetles, and fire exclusion policies). We will build on existing work, including the 2012 publication A Range-Wide Restoration Strategy for Whitebark Pine Forests and existing simulation areas within critical whitebark pine habitat. This project will create a robust and trans-boundary set of management tools for creating resistant and resilient whitebark pine forests within the Rocky Mountains, USA and Canada.

Time frame: GNLCC/USFWS FY13 funded $68,955.

Title: How younger whitebark pine will increase or decrease when the older whitebark pine component dies off.

Collaborators: Erin Shanahan

Objectives: Application of tree ring data

Products: Masters thesis

Time frame: Ongoing

Title: Relating Climatic Data to Whitebark Pine Cone Production in the Custer National Forest, MT

Collaborators: Phillip Farnes (retired), Stewart, and Ann Rodman (YNP).

Objectives: Climate change model to predict whitebark pine cone production in the GYE (Custer NF is pilot). YNP monitoring effort of whitebark pine transects (I&M program is a different endeavor)

Products: results to be presented at WBEF Annual Meeting in Bozeman, MT 9-20-13.

Time frame: Ongoing

Title: The influence of anthropogenic nitrogen deposition on species interactions and ecological resilience

Collaborators: Mailea Miller-Pierce, PhD Student WSU-Vancouver, IGERT. School of Biological Sciences, Vancouver, WA 98686 707-227-6623 m.miller-pierce@email.esu.edu. John Bishop (advisor) Steve Cook (UI) is a committee member due to MPB component.

Objectives: Apply nitrogen fertilizer around the drip line of whitebark pine on the Payette NF (BTIP), other zones? To simulate increased nitrogen availability due to climate warming and impact on mountain pine beetles.

Products: Dissertation

Time frame: 2012+

Title: RIM Board

Collaborators: Linda Vance, Ph.D. |Senior Ecologist/Spatial Analysis Lab Director |Montana Natural Heritage Program (http://mtnhp.org) | P.O. Box 201800, 1515 East Sixth Ave., Helena, MT 59620-1800 | (406) 444-3380 (Helena); (406) 243-5196 (Missoula); (406) 437-1083 (Mobile) | (406) 444-0266 (fax) |livance@mt.gov. Tobalske, Claudine [mailto:Claudine.Tobalske@mso.umt.edu]

Objectives:

Products: Only through association. One of the members of the NASA proposal team is Kathi Irvine, a statistician for the USGS, who is part of the WBP working group with the GNLCC and works on their projects. The Climate Change Analysis, if I recall correctly, is using Rick Lawrence's original classification (~2000, with a red/dead update in 2005) as its basis. What Kathi, Rick & want to do is extend the WBP classification beyond the GYE to the other R1 forests, and then use a different method (object classification rather than pixel classification) to cull out certain elements, namely the regeneration areas and the seed trees, if possible.

Time frame:

Overall project management will be provided by P.I. Linda Vance, Director of the Spatial Analysis Lab (SAL) at the University of Montana in Missoula. Dr. Vance will oversee execution of the plan of work, will act as a formal liaison with partner representatives, and will be responsible for reporting, accountability and budget management. Technical expertise in application of the single-species classification models will be provided by Co-P.I. Rick Lawrence, Director of the Spatial Sciences Center (SSC) at Montana State University in Bozeman. Dr. Lawrence will provide onsite training and phone and email support for image analysts at the SAL during stage 1 of this project. Technical expertise in application of the object-oriented classification of seed trees will be provided by Team Member Claudine Tobalske of the SAL. Dr. Tobalske will also provide day-to-day management of remote sensing activities at the SAL, and will act as the technical point of contact with Dr. Lawrence. Other Team Members will include Melissa Hart, who will act as day-to-day partner liaison, and will take the lead on dataset inventory and acquisition; and Ute Langner, who will perform image analysis activities. We expect to hire a GIS technician to work with the whitebark pine datasets.

Title: Improving understand of threats to whitebark pine in the western US: quantifying climate change effects on mountain pine beetle outbreaks

Collaborators: Jeffrey A. Hicke, Department of Geography, University of Idaho, Moscow, ID 83844-3021, (208) 885-6240 jhicke@uidaho.edu , Polly Boutte (UI), Haiganoush K. Preisler (USFS), USFS Western Wildland Environmental Threat Assessment Center, USGS Western Mountain Initiative

Objectives: Develop a model of mountain pine beetle outbreaks in whitebark pine using observation of beetle-killed trees, climate and general tree conditions.

Products: The model will be used to map the probability of outbreaks in current climate conditions, as well as in future climate change scenarios. This study will increase the understanding of climate/beetle relationships and produce estimates of the future vulnerability of whitebark pine to guide resource managers' decisions on conservation and treatment efforts.

Preisler, H. K., Hicke, J.A., Ager, A.A., Hayes, J.L., 2012. Climate and weather influences on spatiotemporal patterns of mountain pine beetle outbreaks in Washington and Oregon. Ecology 93, 2421-2434.

Time frame: Ongoing to be completed CY13 (Polly Boutte)

Appendix II. Inland West five-needle pine blister rust resistant traits in artificial inoculation trials (Mahalovich 2010, Mahalovich *in prep*).

Blister Rust Resistance Traits[1]	Description
Family level (plot mean)	
Spots per meter	Reduced needle spot frequency; total number of spots on one upper fascicle per average needle-fascicle length
Early stem symptoms	Reduced number of early stem symptoms (cankers) expressed as the number of stem symptoms in the second inspection relative to the number of stem symptoms in the fourth inspection
Bark reactions	Increased callus formation walling off cankers and thereby preventing further infection
Canker tolerance	Persistent seedling growth with active cankers
Individual-tree level	
No-spot	No spot symptoms on needles and no subsequent canker development (only trait to infer immunity)
Needle shed	Seedlings drop their infected (spotted) needles less than 12 months after inoculation and before the mycelium reaches the stem
Short shoot	Seedlings retain their infected (spotted) needles beyond 12 months after inoculation, but never develop a canker (mycelium does not enter woodier bark tissue at the base of the needle fascicle or junction of the short shoot and needle fascicle bundle)
Bark reactions	Increased callus formation walling off cankers and thereby preventing further infection

[1] Resistance can also expressed as the percentage of seedlings exhibiting no-spot, needle shed, short shoot and bark reaction traits for contrast to reports from other screening programs.

Appendix III. Whitebark pine blister rust and mountain pine beetle 100-tree survey form (rev. 04-2003).

Whitebark Pine Blister Rust & Mountain Pine Beetle Survey Form

Field Tally Sheet Sheet

AREA NAME ____________________

STAND NUMBER ____________________

BLISTER RUST

CANKERS PER TREE CATEGORY	TALLY LIVE TREES PER CATEGORY	TOTAL NUMBER OF LIVE TREES PER CATEGORY	TALLY DEAD TREES PER CATEGORY	TOTAL NUMBER OF DEAD TREES PER CATEGORY	TOTAL TREES PER CATEGORY	AVERAGE CANKERS PER TREE FOR CATEGORY	TOTAL TREES x AVG CANKERS
0						0	
			TOTAL TREES WITH 0 CANKERS >				
1-9						5	
10-20						15	
21-40						31	
41-75						58	
76-150						113	
150+						150	
			TOTAL TREES WITH CANKERS >				

Notes:

TOTAL TREES SURVEYED (Trees with 0 Cankers + Trees with Cankers) > ______

< SUM OF TOTAL TREES x AVG CANKERS ______

TOTAL TREES WITH CANKERS / TOTAL TREES SURVEYED x 100 = Percent of Stand Infected with Blister Rust ______

SUM OF TOTAL TREES x AVG CANKERS / TOTAL TREES SURVEYED = Stand Average Number of Cankers per Tree ______

MOUNTAIN PINE BEETLE

TALLY LIVE TREES WITH MPB HITS	NUMBER OF LIVE TREES WITH MPB	TALLY DEAD TREES WITH MPB HITS	NUMBER OF DEAD TREES WITH MPB HITS	TOTAL TREES WITH MPB HITS

TOTAL TREES WITH MPB HITS / TOTAL TREES SURVEYED x 100 = Percent of Stand Infected with Mountain Pine Beetle ______

SURVEYOR ____________________ DATE ____________________

Tally Sheet - Print for Field | Auto Calc - Input Yellow